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Warble flies, Hypoderma Lineatum, Villers, and Hypoderma Bovis, DeGeer, Ottawa, 1919.

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The Principal Differences Between the two Flies.

H. bovis.	*H. lineatum.*
1. Length 14 mm. Distance between eyes just in front of ocelli 1·9 mm., greatest diameter of eye 1·9 mm.	Length 12·7 mm. Distance between eyes just in front of ocelli 1·9 mm., greatest diameter of eye 1·6 mm.
2. Yellow hair on anterior part of thorax.	Anterior part of thorax black and shining.
3. Wing veins dark brown.	Wing veins nearly black.
4. Alulæ have a reddish brown border.	Alulæ are uniformly white.
5. Under part of abdomen and thorax nearly black.	Under part of abdomen and thorax lighter.
6. Legs clean with few hairs.	Legs rough and hairy.
7. Colouring of tail end, orange yellow.	Colouring of tail end, reddish orange.

Methods of Oviposition.

1. Lays in sunshine, principally from 10 a.m. to 4 p.m., but has been seen both earlier and later.	Lays principally in the shade of the animals, from about 10 a.m. to 4 p.m.
2. Causes cattle to "gad," both old and young.	Causes annoyance especially to young animals.
3. Lays its eggs principally when the animals are running.	Lays its eggs mostly when the animals are recumbent.
4. The eggs are laid mostly on the outside of the hind quarters and on the legs above the fetlocks.	The eggs are laid on all parts which the fly can reach when resting on the ground, *i.e.*, while the animals are lying down. Even when the animals are standing, the fly is able to lay eggs on those hairs which are close to the ground, namely, on the heels.
5. The fly is a clumsy insect and strikes at the animals blunderingly.	The fly is much more gentle and deliberate in its movements.
6. The eggs are laid singly at the roots of the hairs and are rarely visible without lifting the hairs.	Several eggs are attached to a single hair and are often visible without lifting the hair.

Skin Lesions.

Hypodermal rash. An irregular scattering of round raised lumps, especially on the outside of the hind quarters, appearing suddenly, anaphylactic in nature and rarely tending to suppurate. Very little exudation of serum.	Hypodermal rash. Diffuse irregular swellings, very irritable, appearing suddenly, anaphylactic in nature, often large and ending in the production of pus, and a marked dermatitis. The lesions follow the parts of the animal which come in contact with the ground, *i.e.*, legs, flanks and sternum. A large quantity of exudate mats the hairs.

Larva.

The segment in front of the spiracular segment unarmed.	The segment in front of the spiracular segment armed.

Summary.

Hypoderma lineatum lays its eggs as early as April 15, but the usual laying period is during the month of May. At Agassiz, they have never been captured later than May 30. *H. bovis* begins to lay in the early part of June and continues up to the beginning of August. Between the last appearance of *H. lineatum* and the first of *H. bovis* there is usually a period of ten days when the cattle are immune from attack of either species. *H. bovis* frightens the cattle much more than *H. lineatum*. The eggs take about a week to hatch; the larvæ bore through the skin in the coarser, porous parts, taking several hours in the process; at this stage they are about 1 mm. long. The lesions

resulting from this penetration are caused partly by anaphylactic reactions and partly by bacterial invasion, those produced by *H. lineatum* being the more severe.

For the skin lesions the name of *hypodermal rash* has been proposed.

At this point there is a hiatus in the life history. It is not positively known how the larvæ reach the œsophagus, where they are subsequently found; most likely they travel in the loose connective tissues under the skin up to the region of the throat and into the œsophagus where the muscles bifurcate. Passing down the œsophagus they follow the submucosa and are almost always found lying along the long axis of the canal. Whilst in the œsophagus, small œdematous swellings are found surrounding the grubs; these are sterile and are anaphylactic in character; the exudate contains large numbers of eosinophilic leucocytes.

The earliest record made at Agassiz of larvæ in the œsophagus was on August 15, when a larva 3·4 mm. was found and several slightly larger. Continental observers have recorded smaller larvæ than this.

H. lineatum makes its appearance in the backs of cattle about December 15, and *H. bovis* about a month later. The larvæ at this time have grown to about 1·5 cm., and are similar in size to those which are found in the neural canal and under the skin. At this stage it is difficult to separate the larvæ of the two species, but Bishopp has, recently, discovered good distinguishing marks between them. The life histories overlap at this period making it difficult to follow the migration, but in the latter part of the season (the middle of March) the last larvæ to leave the œsophagus are at the paunch end. They pass out under the pleura and go to the neural canal, either up the crura of the diaphragm, or up the posterior border of the ribs entering the canal by the posterior foramen. The larva evidently makes use of the canal as an easy means of access to the lumbar region, the part of the animal which is best suited for passing its last stages within the host.

The larvæ follow connective tissue exclusively and no larvæ have been discovered in muscular tissue.

The mature larvæ leave the animals' backs from the early part of the year up to the first days of July.

The periods for the two species have not been fully worked out; but, judging from what records there are of the pupal period and the time of year the flies are on the wing, *H. lineatum* begins to emerge in February and finishes about May 1. *H. bovis* begins about May 1 and ends approximately on July 1. The average pupal period for *H. bovis* is 32·5 days, and for *H. lineatum* a little less. The duration of the life of the flies is short, seeing that they cannot feed. This life history applies to Agassiz, British Columbia; doubtless in other countries variations will be noticed, but the period spent by the larvæ within the host must be of the same duration, seeing that animals' temperatures are the same the world over.

Prevention.—Animals should be housed during the heat of the day to prevent the flies laying upon them. Warble grubs should be squeezed out as early as possible during the year. This method will lessen the damage to animals and their hides. If the total eradication of the pest is attempted, co-operative measures must be undertaken.

ACKNOWLEDGMENTS.

I am indebted to Miss E. B. Cramp for assistance in compiling this paper, and to Dr. E. M. Walker for the loan of three of the figures, which were published in the *Canadian Entomologist.*

The original of this book is in
the Cornell University Library.

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Fig. 1.—*Hypoderma lineatum*, Villers.

Fig. 2.—Natural size.

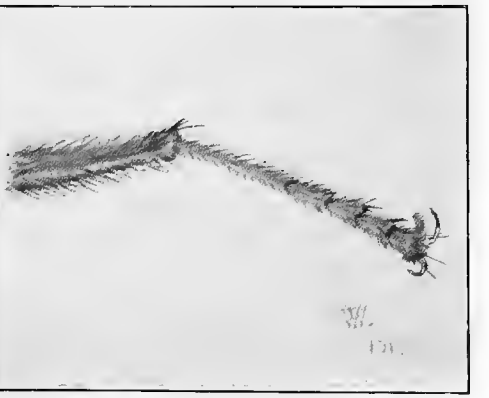

Fig. 3.

DEPARTMENT OF AGRICULTURE—CANADA
HEALTH OF ANIMALS BRANCH

SCIENTIFIC SERIES, No. 27

WARBLE FLIES

HYPODERMA LINEATUM, Villers
and
HYPODERMA BOVIS, De Geer

By

S, HADWEN, D.V.Sc., F.E.S.
Chief Animal Pathologist
OTTAWA, ONTARIO

Published by the authority of the Minister of Agriculture

JULY, 1919

OTTAWA
J. DE LABROQUERIE TACHÉ,
PRINTER TO THE KING'S MOST EXCELLENT MAJESTY
1919

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To the Honourable,
The Minister of Agriculture.

SIR,—I have the honour to submit to you a report on Warble Flies, by S. Hadwen, D.V.Sc., F.E.S., Chief Animal Pathologist, Biological Laboratory, Ottawa, and request that same be printed as Bulletin No. 27.

I have the honour to be, sir,
Your obedient servant,

F. TORRANCE,
Veterinary Director-General.

OTTAWA, September 8, 1919.

INTRODUCTION.

The investigations here described were started in 1911, at Agassiz, British Columbia; since that time a number of papers on Warble flies have been published by the author.

As these papers are now out of print, at the suggestion of Doctor Torrance, Veterinary Director General, the subject matter has been summarized and enlarged to form the present bulletin, which includes many of the original illustrations.

The object of the experiments was to discover expedients to reduce the number of Warble flies and, consequently, the damage they occasion. In this connection, it is interesting to note that, owing to representations made by the War Office to the Board of Agriculture and Fisheries, an attempt is now being made in England to eradicate Warble flies in certain districts. The advisory committee chosen consists of Sir Stewart Stockman, Professor Carpenter, Mr. Fryer, Professor Macdougal, and Mr. Seymour-Jones.

The amount of damage caused, annually, in Canada, is very great. Figures obtained from the principal tanners show that 27·5 per cent of our hides are injured every year. In addition to the hides, how much milk is lost, how much flesh, must be left to the imagination, as there is no reliable method to compute these losses.

It is to be hoped, however, that, when the reader has scanned through these pages, he will gain an idea of the magnitude of the problem that is before us.

To conclude, mention should be made of those who have, in the past, contributed most to our knowledge of these flies. Bracy Clark's remarkable observations were published in 1796, 1826, and 1827. After him came Brauer, Hiurichsen, Koorevaar, Curtice, Schaupp, Carpenter, Hewitt, and Gläser; among whom, in America, Schaupp, and Doctor Cooper Curtice of the Bureau of Animal Industry, deserve special notice.

Finally, the lines quoted by Bracy Clark will not be out of place as they show that long ago the annoyance and damage which the flies occasion was well understood.

> "I will put the brize-in's tail, shall set him gadding presently."—Old Elizabethan drama.
> "The herd hath more annoyance by the brize than by the tiger."—Shakespeare.

The psychic effect of non-biting flies has also been noted:—

> "Un avorton de mouche en cent lieux le harcèle;
> Tantôt pique l'échine, et tantôt le museau,
> Tantôt entre au fond du naseau,
> La rage alors se trouve à son faîte montée.
> Les plus à craindre sont souvent les plus petits."—La Fontaine.

DESCRIPTION OF HYPODERMA LINEATUM

Hypoderma lineatum is a fly 12·7 mm. in length, with distinctive tail colouring of reddish orange. The under surface of the thorax and the anterior part of the abdomen are black, the wing veins nearly black and the alulae uniformly white. The lines on the anterior part of the thorax are bare and prominent, and the legs are rough and hairy. The distance between the eyes is 1·9 mm., the same as in *H. bovis*, which is the larger fly. (Plate I, figs. 1–3.)

Seasonal Prevalence.

H. lineatum can withstand comparatively cold weather and occasionally has been seen ovipositing on cloudy days. In 1915, at Agassiz, the first flies were taken on April 15, and several more on April 22, 23 and 24. The period during which *H. lineatum* was active was eighteen days, and flies were either seen or caught on nine of those days. The only correspondingly early record seen in European literature is by Imms, who examined specimens in the British Museum and says that the specimens in the collection have dates varying from the end of April to the beginning of June. The deficiency, both in Canadian and in European literature, is probably due to the fact that the earlier fly, *H. lineatum*, causes so little annoyance to cattle, that collectors have not looked for it.

Oviposition and its Psychic Effect on Animals.

H. lineatum irritates cattle much less than *H. bovis*; in fact, when gentle animals are being attacked, the disturbance among them is often very slight

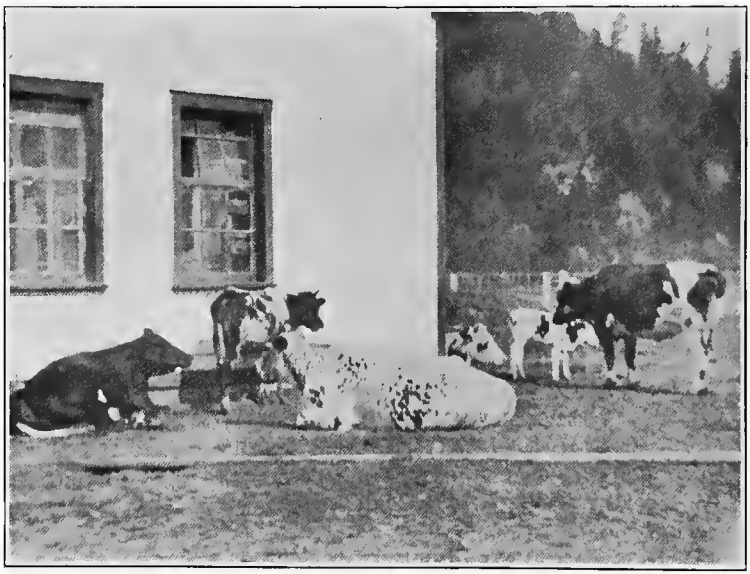

Fig. 4.—*H. lineatum* ovi-positing on the spotted cow in the foreground. Note contented look of animals.

and may pass unnoticed by the casual observer. On the other hand, wild (range) animals, free to go where they please, exhibit a good deal more annoyance. Among gentle cattle the young ones will sometimes run or gallop, but the older

animals, though they may occasionally lift their tails and perhaps run a short distance, are often so indifferent to the irritation caused by egg-laying that they will merely stamp or whisk their tails. These remarks only apply if egg-laying takes place on standing animals, for when animals are in this position, it is necessary for the fly to grasp the hairs to oviposit, with the exception of those hairs, which are about the heels, which can be reached with the ovipositor while the fly is resting on the ground. The fly has a habit of settling under the shadow of the cow's heel and it can often be seen running backwards and lifting up its ovipositor, attaching its eggs to the coronet. Other favourite places for egg-laying are in the regions of the fetlocks of the fore and hind legs, and also on the knees and hocks. Flies are seldom seen ovipositing higher than this on

Fig. 5.—Fly ovipositing on cow's tail.

a standing animal, though in fig. 5 a fly may be seen ovipositing quite high up on a cow's tail. The fly alights on the animal quite gently and since it lays a number of eggs in sequence on a hair it must necessarily cause the animal but slight annoyance in order to do so.

Seeing that oviposition takes place principally when the animals are resting, the insect has a much better opportunity for laying where it likes. The line of contact of the animal's body with the soil is where most eggs will be found. From before backwards, the line extends from the sternum, along the flank to a point about six inches below the ischium. The udder is also a favourite place for egg-laying, and another spot is just behind the elbow. In this case, the fly runs up the hoof which is tucked in under the elbow; when it reaches the top it backs up and pushes its ovipositor among the hairs. *H. lineatum* invariably lays with its head pointing in the same direction as the hairs. (Fig. 5.)

In searching for the fly among recumbent animals, it is well to look underneath them in the shady parts. A fly will often remain with an animal for

fifteen or twenty minutes, and in some cases a good deal longer. The only irritation noticeable in such a case may be an occasional raising or shifting of the body, or perhaps the tail may switch a little, but the annoyance is not sufficient to make the animal rise. The time of egg-laying is during the warmest part of the day, usually from 10 a.m. to 4 p.m.

The Egg.

The egg is cylindrical, yellowish white, with a pedicel by which it is attached to the hair. The number of eggs on a single hair varies, as many as fourteen having been found. (Figs. 6, 7.)

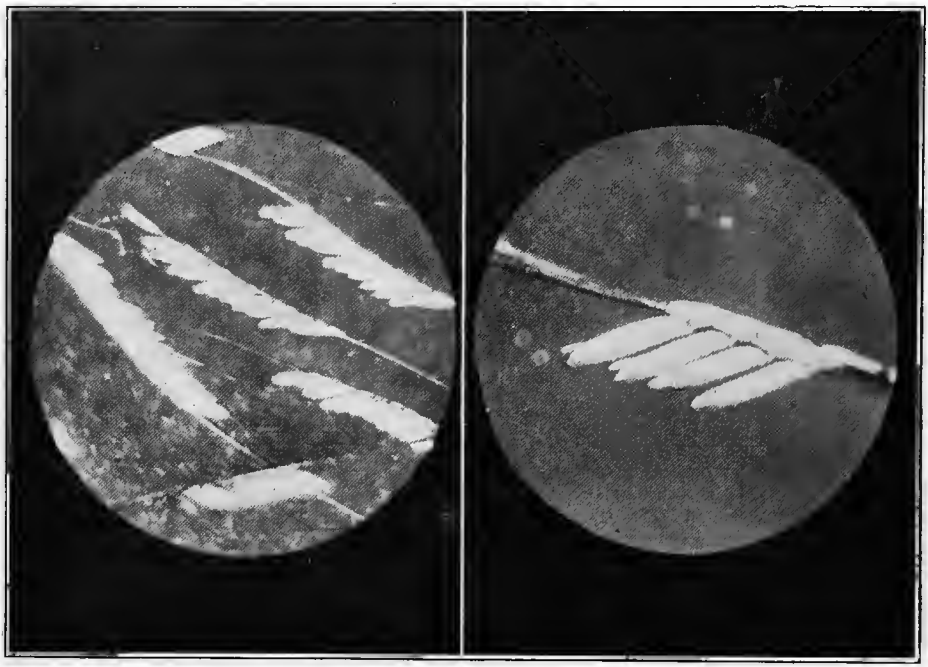

Fig. 6. Fig. 7.

Eggs of *H. lineatum.*

The eggs are often in full view; this is because eight or ten eggs in sequence take up a considerable space on the hair.

The time taken for eggs to hatch is about seven days, the shortest period being four or five days. Eggs, which are removed from an animal, hatch readily under varying conditions; they have been hatched with and without moisture, and with and without heat.

The Larva.

Larvae have been seen in the act of emerging from the egg on several occasions. In one experiment, eggs were taken from an animal together with a portion of the underlying skin. This was done at 11.45 a.m. A larva hatched at 12.15 p.m., a second at 2, and a third at 4.45. It is interesting to note that the egg next to the skin hatched first and the other two in order. This is probably due to the fact, that those nearest the skin had been laid first, and also that those nearest the body derive most heat.

Method of Penetration.

Upon emerging from the egg the larva crawls actively along the hair to the skin. It is apparently aided in this by a sticky exudate with which it is covered, which seems also to serve the purpose of preserving it from drying out. Upon reaching the root of the hair, it begins to work with its mouth parts. In no instance was a larva observed to penetrate the skin otherwise than by way of the hair follicle. The adherence of the larva to the hair keeps it in proper position for penetration and provides it with a *point d'appui*.

Hewitt in 1914, who was the first to observe this penetration, saw several larvae of *H. bovis* penetrate the skin, and Carpenter, Hewitt and Redden mention

Fig. 8.—Larva of *H. lineatum* penetrating a hair follicle.

Fig. 9.—Enlargement of larva shown in Fig. 8.

the difficulty of watching the larvae on a live animal. They say, "it took the larvae about six hours to get into the skin; possibly the hair follicles may have facilitated entrance." The actual penetration of the skin by the larvae of *H. lineatum* was not observed by them. Since that time the penetration of the skin by the larva has been amply verified; and, at Agassiz, larvae have been discovered in the act of burrowing into the skin.

Seeing there has been so much controversy on this subject, all the first experiments are here republished in full, just as they were made in 1915:—

1. Twelve larvae, which had just hatched, were placed on a calf's back. They worked actively, but none of them succeeded in going through the hide during the period of observation, 10.30 a.m. to 11.15 a.m. The larvae worked so slowly and there was so much difficulty in keeping the calf quiet, it was decided to abandon this method.

2. A small piece of skin was removed from an animal and five larvae placed upon it. Two of these made determined efforts to pierce the skin, and about 1 p.m. had succeeded in getting half way in. The skin was then placed in an

incubator at 88°F.; at about 2.30 the larvæ were apparently dead. Another experiment was made on the following day and of twenty-three larvæ placed on the skin at 3 p.m., one had just disappeared from sight at 9.30 the following morning; by 2 p.m., the same day, one larva had completely penetrated the hide, and three others were three-quarters of the way in.

3. A third experiment was made to try and discover the natural penetration of the skin by larvæ hatched on the cow. A small piece of skin, on which eight eggs were attached to a hair in the centre, was cut off a cow's udder. Six of the eggs were hatched and two unhatched. There was a slight amount of subcutaneous inflammation. The hairs around this spot were clipped off, leaving only the hair to which the eggs were attached. A larva was found close to this point actively working and penetrating the skin. (Figs. 8 and 9.) The experiment commenced at 3.45 p.m.; at 10.20 p.m. the larva was nearly three-quarters of the way in, but at 8 the following night, it had not disappeared from sight. Repeating the previous experiment, a piece of skin underlying three hairs, to which twelve eggs were attached, was removed from a cow. Nine of the eggs had hatched. At the foot of one of the hairs a droplet of clear serum was exuding and kept increasing in size; evidently some force was expressing it. On the piece of skin being grasped with strong forceps and bent double, a larger flow of serum resulted and eventually two larvæ were pressed out. One of these was extremely active and endeavoured to re-enter the hair follicle from which it had come.

The larvæ were no doubt placed at a disadvantage in the experiments where the skin was removed; for, in the first place, it is probable that the skin movements of the living animal may aid larvæ to penetrate; secondly, when working on skin which has been removed from the living animal less serum exudes, though the piece of skin be kept constantly moistened underneath; thirdly, putrefactive changes occur. Soon after the larvæ have gone under the skin there is an outpouring of serum from the openings through which they have entered. It may be that several larvæ go through the same opening, seeing that when they descend the same hair to which the eggs are attached they all land at the same point. But this has not been proven. The reaction on the part of the animal against this penetration is much more pronounced in the old animals than in the young, no doubt owing to the fact that the former have become sensitive to the larval secretions and excretions during previous infestations. The swellings are thus reactions against parasites and account for the smaller number which mature in the old animals as compared with the young. These skin swellings are irregular in shape and sometimes attain large dimensions; when the swelling subsides it will be found that portions of the skin have become necrotic and a scab has formed. When this scab is lifted off, one or more conical pits will be discovered filled with yellow pus. This pus has been examined and is found to consist almost entirely of a variety of a white blood cell, known as the eosinophile. This cell has the special function of attacking parasites, including worms, and no doubt plays a very important part in the destruction of larvæ.

The name of hypodermal rash has been proposed for these skin lesions. They are naturally seen in the regions where the eggs are laid, and figs. 11-14 show where they may be found.

Following the penetration very little is known about the migration of the larva. However, early in August, larvæ have been found in the walls of the oesophagus, but by what route they have reached this point is not known; most likely they travel in the loose connective tissues to the region of the throat and into the oesophagus where the muscles bifurcate.

Migrations of the Larvae Through the Tissues.

The young larva having penetrated the skin, arrives in time at the gullet. (Fig. 10.)

Note.—Hadwen, S., and Bruce, E. A., 1916, Observations on the Migration of Warble larvæ through the tissues. Dom. Dept. of Agr. Bulletin No. 22.

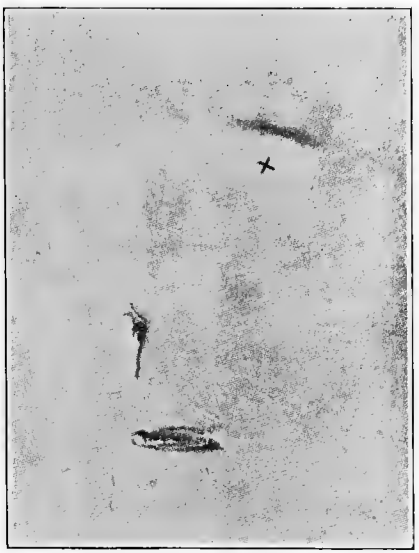

Fig. 10.—Larva in œsophagus. Mucous membrane incised to show larva. The shadowy outline of another larva may be seen at the point marked +.

What route it follows has not been ascertained, though it would seem highly probable that it makes its long journey exclusively through the connective tissues. It has been suggested that the larvæ might reach the anterior part of the body by the blood stream, but this seems unlikely. It has been proved by observation that the larvæ follow the connective tissues very closely, and a number of experiments were made with larvæ, which had been extracted from cows' gullets. These larvæ were dropped into small pockets made under the skin. In one case a pocket was made on the right hand quarter of a calf and twelve larvæ were dropped in; subsequently, four of these larvæ reached the animal's back.

In another experiment made on January 25, 1914, twenty-five larvæ were placed in a pocket on the left hind quarter of a November calf, and on February 2nd, several of the grubs had reached the back, and later, eleven of them pierced the skin.

In another experiment, November 17, 1914, with a three weeks' old calf, five larvæ were slipped under the hide on the outside of the knee; twenty days later, two of the larvæ had punctured the skin on the calf's back. The calf was killed and the leg skinned. A gelatinous track was found at the point where the larvæ had been introduced, viz., on the outside of the knee, at a point over the tendons of the extensor muscles. Following this track it was found to extend in towards the radius, passing round it posteriorly, upwards under the elbow joint to the scapula. A larva was found about two-thirds the way up this bone, near the posterior border, that is to say, under the sub-scapularis and above the serratus magnus. The track was plainly visible in the white fibrous tissue.

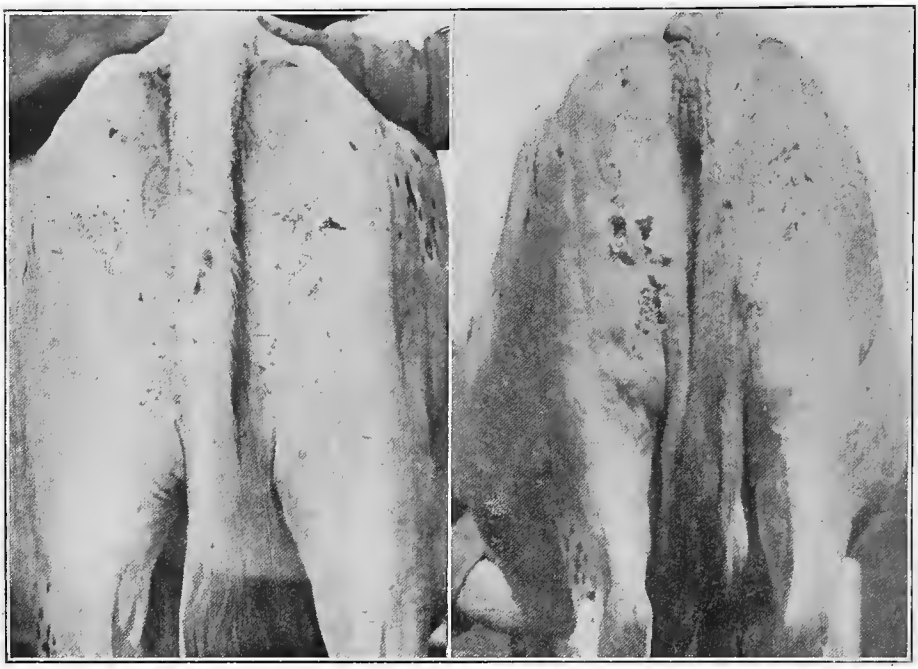

Fig. 11.—Lesions of the skin caused by the extrance of Warble larvæ. Note the lesions on the tail.

Fig. 12.—The same animal two days later.

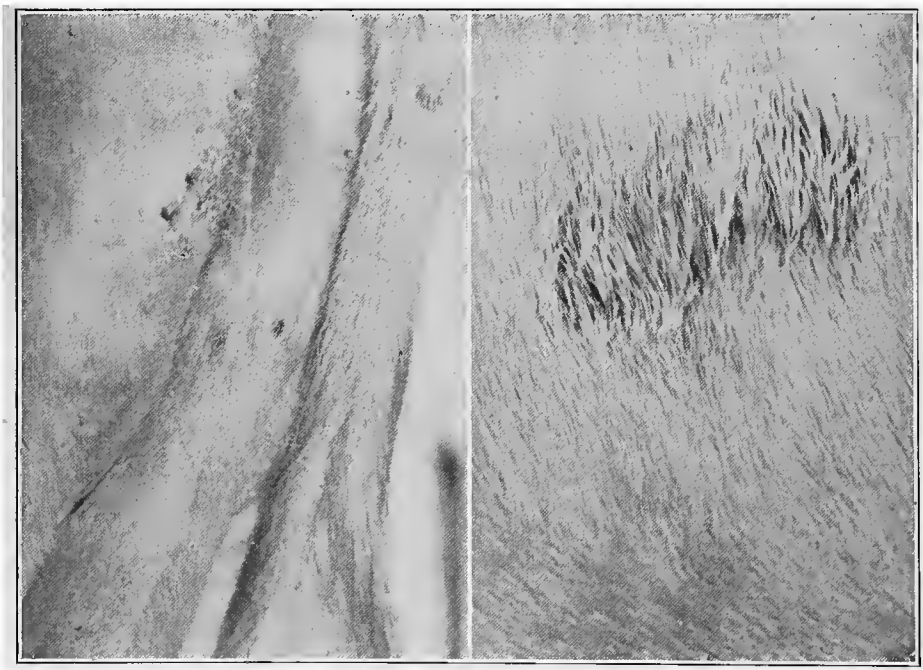

Fig. 13.—Lesions on cow's udder.

Fig. 14.—Circular spots after the larvæ have entered. An exudation of serum has matted the hairs.

These experiments show that the larvæ choose the easiest and the most non-vascular tissues in their migrations, and it would seem probable that even when they are newly hatched, they would have the same habits that they adopt in their later migrations.

If, then, this is correct, in all probability they gain entrance to the œsophagus in the region of the throat.

In a large number of gullets, which were examined at regular intervals throughout the winter of 1914-1915, it was found that the larvæ move up and down the gullet continuously, that the greatest number were found in the gullets during December, and that they gradually diminished in numbers until the month of March when they disappeared from this region. Hiurichsen, Koorevaar in Europe, Curtice, in America, and recently, Carpenter, in Ireland, have obtained very similar results.

The last larvæ to leave the gullet were at the junction of the œsophagus and the paunch, where the muscle fibres are widely separated, and have a radiating arrangement. This is undoubtedly the place where the larvæ would start on their journey to the back. They were here found going in different directions. At this point there is a reflection of the pleura over the end of the gullet, beneath which they could readily pass up the crura of the diaphragm, or else take a longer course along the posterior borders of the ribs.

On finding that the larvæ were disappearing from the œsophagus, attention was next directed to tracing them in their subsequent migrations. Apart from finding the larvæ leaving the œsophagus at its junction with the paunch, very little is known about their route to the neural canal, except that gelatinous tracks were noted by the author, which were very likely caused by them. Other observers have occasionally encountered larvæ between the gullet and the neural canal. Curtice found some under the pleura in the region of the eleventh rib, and Ransom has a larva which was discovered under the pericardium.

Direct evidence has been secured that the larvæ make use of the posterior foramen to gain entrance to the neural canal. In the neural canal itself, a considerable number of larvæ have been found, as many as seven larvæ have been counted in one animal; also several larvæ were discovered just emerging from the posterior foramen. The larvæ are found in the soft areolar tissue, which surrounds the dura mater. The presence of the larvæ in the neural canal causes a gelatinous infiltration and a greenish pigmentation. The fat also exhibits grey degenerate areas, which is evidence that the larvæ cause irritation and that there is a reaction against them.

All stockmen are familiar with the appearance of the mature larva. When it first reaches the back, it is whitish, about 1.5 cm. long; when, however, the larva is mature and ready to leave the back it measures about 2.5 cm. and has changed to a grayish black colour.

Suggestions for the Complicated Life History Within the Body.

There are various reasons which suggest themselves as to why the larvæ select different portions of the body, in which to pass certain stages of their existence. In penetrating the skin, for example, it will be noticed that they choose the coarser and more porous parts to penetrate. The gullet where they are next found, appears to be admirably suited to them as a habitat during the autumn months. The parts they live in are only slightly vascular, hence the reaction against them is not as great as it would be in other tissues, but the reason for their constantly being on the move is evidence that there is such a reaction; and if a number of gullets are examined, it will be seen that the larvæ are often surrounded by œdemas.

In other cases, one can see that the larva has just moved away from the inflammatory area, or else is just beginning to do so.

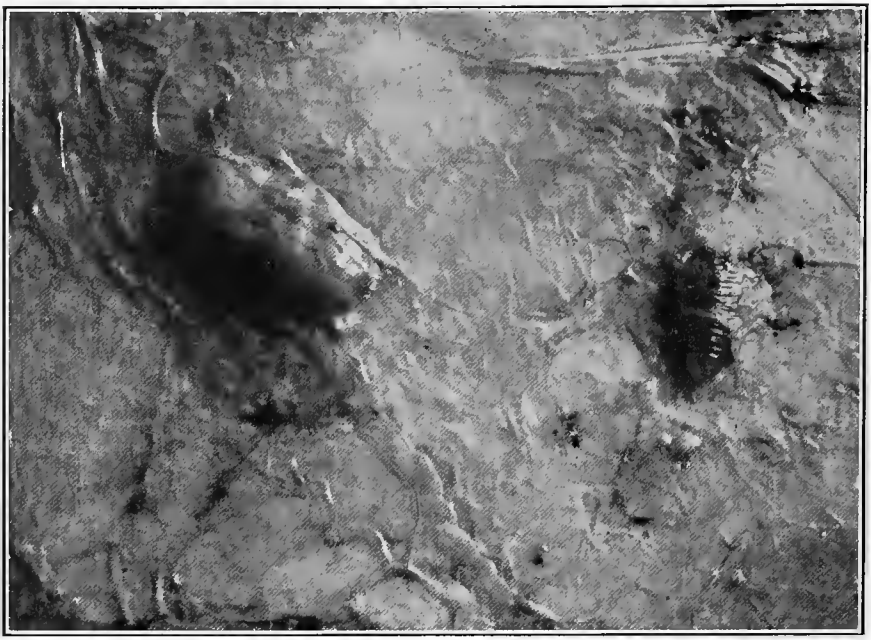

Fig. 15.—The under side of a cow's hide showing (on the right) a partial dissection which reveals a young larva lying horizontally and (on the left) an unopened Warble.

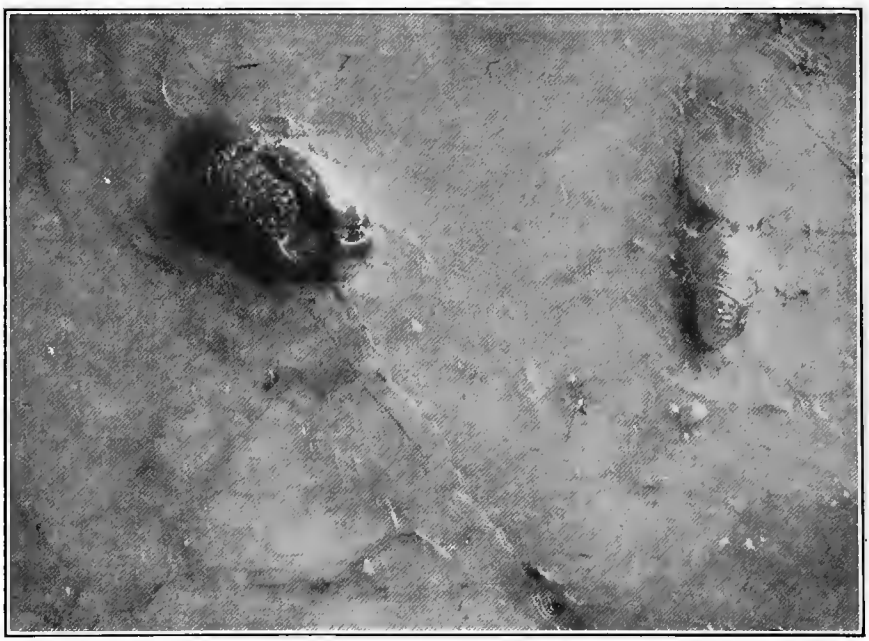

Fig. 16.—The same specimen shown in Fig. 15, the Warble on the left having, however, been partially dissected so as to reveal the position of the larvæ.

FIG. 17. [redacted] De Geer.
Hypoderma bovis,

FIG. 18. Natural size.

FIG. 19.

These swellings have been carefully studied and the principal cell encountered in them is the eosinophile.

The migration from the gullet to the back is evidently quite a short process, as larvæ taken from the gullet, the neural canal, and the back of the same animal all proved to be of the same length. The final position taken by the larvæ is in connective tissue, very similar to that found in the gullet. Here again, there is a bodily reaction against them, which is manifested by œdematous swellings. Very probably this reaction would end in their destruction since they have now taken up a fixed position. But, shortly after reaching the back, they bore through the skin, the result being that air gains entrance into the cavity in which they lie. Other factors also come in, such as the introduction of bacteria; consequently, the defence on the part of the tissues against the larvæ will be modified.

During the approach of the larvæ to the back and the period in which they are boring through the skin, the animals suffer a good deal of uneasiness, which is evinced by their constantly licking the region of the loins; and, if a cow stable be visited at this period, it will be noticed that the hair has been well licked in the regions that can be reached by the animal's tongue. After the larva has finished boring through the skin, the œdema of the skin subsides to a considerable extent and the irritation and licking are not so pronounced.

The Position of the Larvæ under the Hide.

The opening through the hide is oblique and the larva lies with its ventral surface upwards. The caudal end is bent and protrudes through the opening, which gives the impression from an outside view that the grub is placed perpendicularly beneath the hide, instead of horizontally, as is actually the case. (Figs. 15 and 16.) The advantage of this position is that the effect of the skin movements is reduced to a minimum.

For a somewhat similar reason, the second stage larvæ lie longitudinally in the œsophagus. The contraction of the longitudinal muscles would simply cause the larva to shorten its body as it does naturally. If it lay transversely, the circular muscles would bend the body sideways.

Time Taken by H. lineatum to Emerge from the Pupa.

According to continental observers, the pupal period is about thirty days. In Canada, it has been proved that with artificial heat this period may be shortened considerably and a fly has emerged in as brief a period as thirteen days and several others in fourteen days.

DESCRIPTION OF HYPODERMA BOVIS.

Hypoderma bovis is a fly 14 mm. in length, with yellow hair on the anterior part of the thorax, dark brown wing veins, and a reddish brown border to alulæ. The under part of the abdomen and thorax are nearly black; the tail end orange yellow and the legs are clean with few hairs. The latter qualification is a distinctive feature for *H. bovis*. The distance between the eyes in front of the ocelli is 1·9 mm. and the greatest diameter of the eye is 1·9 mm. (Plate 4, figs. 17–19.)

Seasonal Prevalence.

H. bovis appears in the early part of June and continues up to the beginning of August. For the years 1912, 1914 and 1915, the average period during which *H. bovis* was active was fifty-six days. In 1915, careful records were kept and

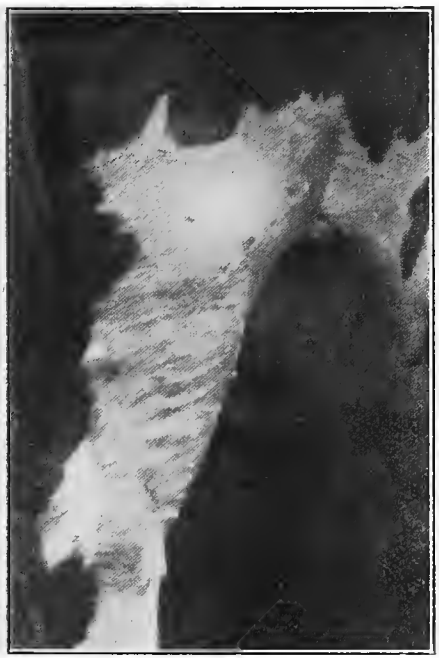

Fig. 20.—Penetration of the skin by the larva of *H. bovis*. Lesions on outside of cow's leg.

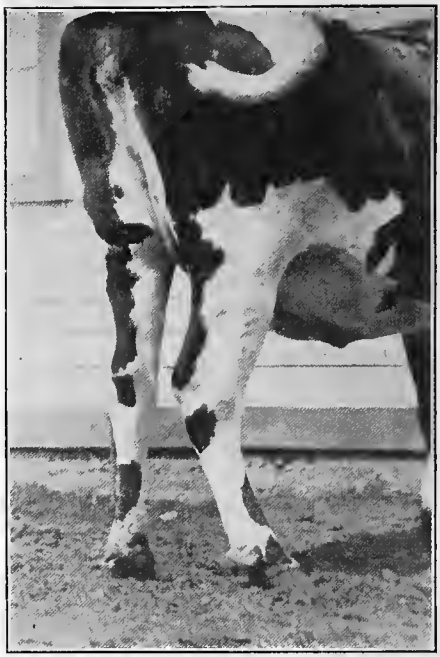

Fig. 21.—Lesions on hindquarters. Note large swelling on left leg behind the udder.

on twenty-eight days out of the season of fifty-five days, flies were either seen or caught attacking the animals. This means that during the season there were twenty-eight days which were favourable to the fly.

These observations coincide closely with the pupal period and with the time the last larvæ emerge from the backs of cattle.

Method of Oviposition.

H. bovis lays in sunshine, generally when the animals are running, on the outside of the hind quarters and on the legs above the fetlocks; if the animal be quiet, the eggs are deposited low down, but higher, as soon as the animal moves (Figs 20 and 21.)

Egg-laying has been frequently observed and, whenever witnessed, never occupied more than a few minutes. It may be described as a frenzied process. Flying about level with the stifle joint, the insect strikes twenty or thirty times rapidly, leaves the animal for fifteen minutes or so, returns and repeats the attack. Sometimes it follows behind, catches up for a moment and drops back to the same position.

As the fly strikes, it hangs on with its legs to a hair for a second, cementing an egg to the root of the hair, rendering the egg invisible unless the hair be raised. An egg, deposited in the natural way, is firmly attached. The groove

seems to be squeezed on in such a way that it opens and grasps the hair; and the sticky material which makes the egg adhere so firmly must be inside the groove when the egg is extruded.

As only one egg is laid at a time on a hair, the fly has no object in finding the exact spot on which it laid a previous egg, and, as the cattle are running,

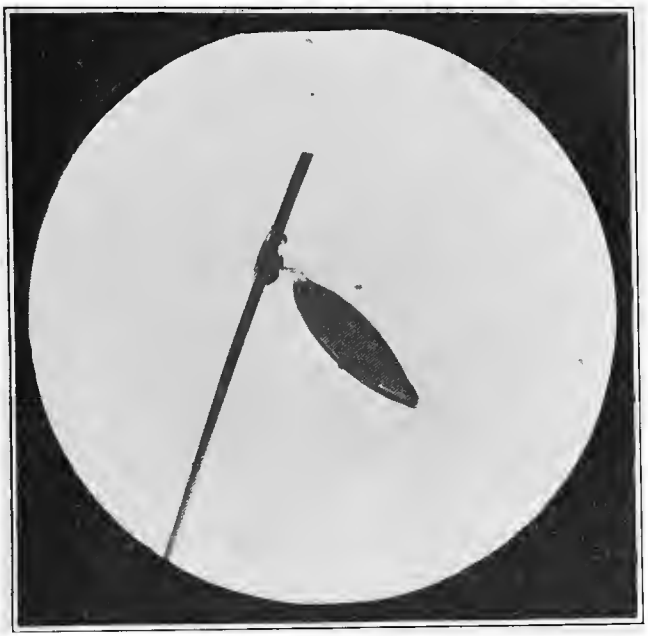

Fig. 22.—Warble-fly egg attached to hair. Much enlarged.

it is perhaps unable to do so. The eggs are thus deposited in an irregular manner as can be seen by referring to the illustrations. The eggs were first discovered in 1912, and the following experiments were carried out.[1]

A day was chosen when the animals were galloping about, and the first thing was to capture a fly. This done, all the animals were housed except the one on which the experiment was to be made. The latter was securely tied to a fence and closely watched as the fly was liberated. The insect, after sunning itself, usually attacked low down on the legs. Whenever it struck, an examination was made; so close was the egg to the base of the hair that it was often difficult to pass a thin pair of scissors between the egg and the skin. (Figs. 22–24.)

Later on, it was found that the best way to observe the method of attack was to put a number of animals in a small enclosure and watch the fly at work.

Experiments were also made in another way. Flies, with their wings clipped, were placed on cows' backs and watched for considerable periods. Though the flies laid a number of eggs they did not attach them to the hairs; presumably, because the wings had been clipped. The eggs which they laid did not appear to be at all sticky, probably on account of the groove not being opened.

To secure a number of fertile eggs, flies were caught as gently as possible, and held by the net on an animal's flank or back. The flies rested on the animal and pushed their ovipositors under the hairs at intervals. The rapidity with which they work is surprising, and a large number of eggs may be obtained in this manner in a comparatively short time.

[1]For the penetration of the skin by the larva, see p. 8.

Fig. 23.—Ovipositor with egg.

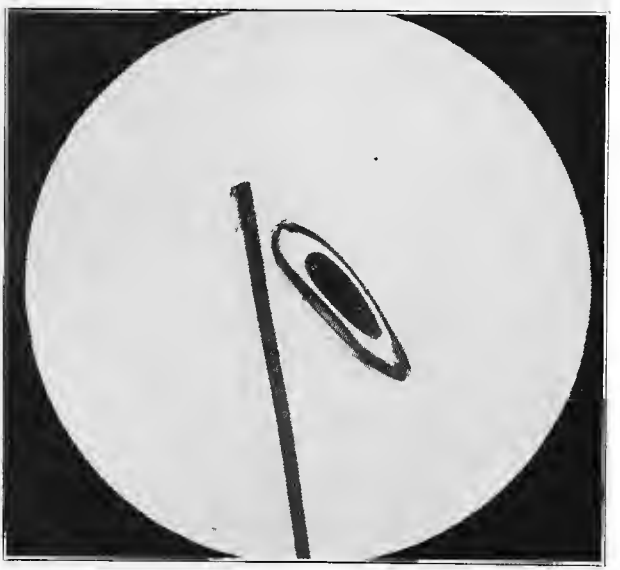

Fig. 24.—Larva inside egg much enlarged.

In these experiments the animals seem to feel little or no irritation during the process; though, on occasions, when the fly buzzed loudly or flew about a good deal, the animals showed uneasiness.

The Psychic Effect of Oviposition on Animals.

The terror-inspiring effect of *H. bovis* has mystified people for a very long time. The fear and terror that it inspires cause cattle to lose their heads completely and the results are often disastrous.

Fig. 25.—Cow being chased by fly. Note terrified look of eyes.

Wild cattle naturally get more panicky, and are less tolerant than gentle cattle. They are also more agile than a fat bullock grazing in a small pasture. Gentle animals on an ordinary farm usually find ways and means of escaping from the attacks of the fly by running into the shelter or shade of buildings and bushes, or into the water. On the prairies, it is quite a different matter, as there are so few trees, and the only chance the animals have is to make for a lake, or river, or else to dust themselves.

The following story illustrates a common incident where cattle are used as work animals. One day in Alberta, a cowboy seemed to be vastly amused about something; and the cause being asked, he said: "Well, I came riding by a little lake just now, and I saw some cattle standing in it with their yokes on; a disconsolate settler was sitting on the bank and said that he was waiting for the animals to come out with the plough, and that he would not get much ploughing done if the flies did not stop chasing his cattle into the water."

When an animal is attacked by a fly for the first time, it allows the fly to oviposit without showing any greater sign of discomfort than the tickling of a straw would occasion. If the fly is persistent, the first noticeable sign is that of annoyance; the animal will stamp or kick and switch its tail vigorously. The next thought the animal has is apparently to move away from the annoying insect, which it does by walking to another place. If a fly continues to pester it, it begins to trot and finally to gallop. When an animal is running in this manner, it will be noticed that it frequently turns its head to try and see if the fly is still pursuing it, and to do so pauses in its flight. If, at this moment, it finds that the fly is still pestering it, the flight will begin again with redoubled energy and with additional terror.

This, in brief, reveals the mental process the animal goes through, and it is easy to see when the fly's methods are studied, what an annoying and aggravating insect it is.

The mental process produced by the Warble fly on cattle is similar to that produced on a bald-headed man by house flies; the feeling of annoyance, followed by anger, is exactly the same, but it should be remembered that *H. bovis* is rougher in its movements and is a much larger fly than *M. domestica.*

A number of experiments have been made on the terror producing effect of the fly. In 1915, a test was carried out on two calves, which had been kept

Fig. 26.—Calves attacked by *Hypoderma bovis* trying to get into a barrel of water.

in doors until the season for *H. bovis*, and were closely watched when they were first liberated. They went through all the phases, which are described above.

There are some other results which follow fly attacks; for instance, if the flies are plentiful and the animals are kept constantly on the move, they naturally become tired; then they seem to regain their senses somewhat, and try to find ways and means of evading the fly, such as in fig. 26, in which two calves are doing their best to get inside a barrel. If the animals become positively exhausted, then they sometimes become quite indifferent to the attacks of the fly and lie on the ground in a fit of stubborness, refusing to move. In other cases, they are plainly endeavouring to hide and make themselves as unobtrusive as possible. In this way, they certainly appear to some extent to escape the attentions of the fly, as it undoubtedly prefers to attack standing animals.

The origin of a stampede.

The terror that the fly produces is contagious, and it suffices that one animal should be attacked to set the whole herd running. In this connection it was interesting to watch the behaviour of the experimental animals which were used. Each animal had different habits and when a Warble fly appeared in the barn yard the alarm spread through the whole herd. They immediately acted upon it; the animal which was attacked of course galloped away; the others all dispersed to favorite corners, or tried to get as far away from the point where the insect was seen or heard.

On a number of occasions, the offending fly was captured and held prisoner for a time; the animals would then quiet down and return to their food, or some shady or favorite spot, and all that was necessary to upset this tranquil scene was to liberate the fly again.

This is a most convincing method of demonstration, and, on a number of occasions, doubting persons have quickly become interested in the fly. Many people have an idea there must be a large number of flies attacking the animals at one time, but in all experiments, and on all the days spent in studying these insects the largest number captured in a single day was six.

It cannot be denied that other flies annoy animals to a very great extent. However, the annoyance is of a totally different character; for instance, though the *Tabanidae* draw much blood and cause painful bites, yet cattle are able to drive them off by switching their tails and, generally speaking, these flies cause them but little annoyance. The same thing applies to the *Simulidae* and to the Mosquitoes. Cattle become exasperated, it is true, when there are a large number of flies about and will frequently dash among bushes or dust themselves, to get rid of them; but, the fear is not contagious and only one or two animals are affected at a time.

Treatment.

Many remedies are recommended for killing or extracting the grubs after they have bored through the skin of the back. The practice of killing the larvæ under the skin by injecting or applying mixtures is unscientific, for if the larva is nearly mature its chitinous cuticle cannot be absorbed, and may be found months later under the hide which has completely healed above.

The best method, undoubtedly, is to squeeze out the larvæ as early as possible, softening the skin first; in this way the wound rapidly heals. In some cases, it may be necessary to enlarge the opening by a slight cut, especially in regions where the skin cannot be properly grasped. The flexibility of the skin also varies according to the condition of the animal.

Prevention.

Though many attempts have been made to exterminate Warble flies in various countries and localities, so far these efforts have met with little success.

The squeezing out of the grubs seems to be a simple matter, but though many cattle breeders perform this operation each year, their animals are quite heavily infested the following season. No doubt the explanation lies in the fact that they overlooked some of the larvæ, either early or late, or it may be that their neighbours' cattle are not similarly treated. As a single fly is capable of laying several hundred eggs, it is quite easy to see how the pest survives from year to year. One point which has never been cleared up is the distance which Warble flies can travel, but it seems likely that they do not go any great distance.

The mixtures applied to prevent egg-laying have proved useless in the past and many of them have been injurious to the hides and to the animals. The older authors recommended farmers to apply dressings to the animals' backs and, in England, a common practice was to smear them with train and fish oil. Seeing that the eggs are not laid on the back, the practice was decidedly useless and costly.

According to Ransom, in the United States of America, arsenical dips appear to have some beneficial effects, but no definite experiments have been published as yet. It has been said that squeezed out larvæ do not hatch, but if the larvæ be sufficiently mature they will do so; therefore it is wise to destroy them after they have been taken out. The eradication of the fly is theoretically possible by the "squeezing-out" method; this would apply to organized districts where every animal could be treated. Among wild animals such as are found on the Western Canadian ranges it would be almost impossible. *In settled districts squeezing out the larvæ and housing the animals during the hot weather should soon bring about a noticeable diminution of Warbles. The animals should be housed from 6 a.m. to 6 p.m.*

Distribution.

In certain districts in Canada the flies are worse than in others; strange to say, in some parts there appear to be none at all. No explanation can be given for this fact; it may be that some climatic variation is responsible for this, in the same way that Australia and South Africa have escaped the fly. Generally

speaking, *Hypoderma bovis* and *lineatum* appear to have an equal distribution all over Canada. How far north these parasites occur has not been ascertained. Bishopp states that *H. bovis* is commoner in the northern parts of the United States of America than *H. lineatum*, and that with regard to *H. bovis* it "must have some well marked climatic barriers which have prevented its general dissemination throughout the country."

The Economic Aspect of Warble Flies.

In 1912, Doctor Torrance, the Veterinary Director General for Canada, addressed a circular letter to the tanners in the different provinces throughout the country to find out what damage was caused by Warble flies. Many letters were received in answer and the evidence collected shows that Warbles damage hides to a very great extent in the Dominion.

As the letters came from sound business men, who had no interest in the matter save to get hides free from Warbles, the information is to be considered most accurate.

The evidence showed that the man who undoubtedly loses is the farmer; the tanner does not want warbled hides at any price, and several of the writers testified that they only bought hides during the autumn season when the hides are not grubby.

The uses a grubby hide can be put to are very limited, and for some purposes, such as the manufacture of belts for machinery, they are practically useless. (Fig. 27.)

Some interesting facts were brought out concerning the grades of hides most affected by Warbles, which can be explained by a knowledge of the life history of the parasite.

In Canada 25 per cent to 30 per cent of all hides are damaged by Warbles.

The length of the Warble season from the tanners' point of view extends from late January to early July, the worst period being the month of April. This statement tallies absolutely with the records kept at Agassiz.

Nearly all tanners agree that the rough, long-haired, ill-kept animals are most "warbley" and that well-fed, sleek animals are not so badly affected. The reasons are not far to seek: first, weak animals are always more parasited than the strong and cannot fight the fly as well as the more robust; secondly, dairy cattle and well bred animals are often housed during the heat of the day, whereas, ill-kept beasts are at the mercy of the fly all day long.

One of the tanners mentioned the fact that northern hides were as a rule thinner and more hairy than southern hides, and the latter, being thicker, may afford the animals some protection from the penetration of the larvæ.

Young animals are more parasited than the old, and, therefore, their skins will naturally be more damaged.

The tanners view a wet season with favour, as the following year will be a better one for skins. The reason for this is quite apparent as the fly is only active in fine weather.

One form of damage to the hide which the tanners have not apparently connected with Warble flies is one which has been mentioned before and called hypodermal rash; the scab formation, and pits made by the larvæ in penetrating the skin must necessarily destroy the grain of the leather.

Systemic Effect on Animals.

The systemic effect on the animals is very hard to gauge though badly warbled animals certainly do not look as healthy as clean animals; whether an animal's growth be stunted or not is difficult to prove and definitely controlled experiments are needed to decide this point. The same thing applies to milk

yields; that the larvæ do cause some effect on an animal is proved by the fact that they are sensitive to the protein contained in the parasites.

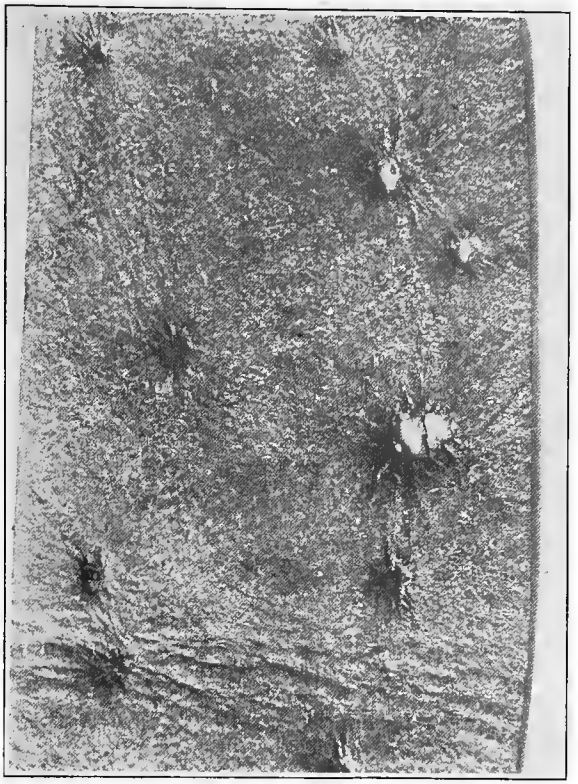

Fig. 27.—Actual size of leather, $3\frac{1}{4}$ in. x $3\frac{3}{4}$ in.

The poisonous qualities of warble juice have been proved by a number of experiments. (Figs. 28 and 29.)

When the juice derived from the larvæ is injected into a sensitive animal, that is, one which has been harbouring the parasites, the reaction termed anaphylaxis is frequently produced. The reaction occurs in two forms, one, which is rapidly fatal, kills the animal in a few moments; the other, appearing in twenty minutes to half an hour, causes grave symptoms followed by recovery. The amount of material which is necessary to produce the effect appears to be very small; in one case, a full grown cow was killed with the juice of three and one half larvæ. In other cases, larger amounts were used; but, as stated before, the degree of sensitiveness in the animal appears to be more important than the size of dose which is administered. In the rapidly fatal attacks, the most marked symptoms noted were those of asphyxia. In the non-fatal cases, œdemas occurred in many parts of the body and also a marked wrinkling of the skin. Blood may be passed from the natural openings. Cases of anaphylaxis have also been diagnosed in animals, which had not received any injection. These cases occurred in dairy animals and were probably produced through injury to the warbles on their backs. In two cases, there was a definite history of such injury. A number of reports from Veterinarians have also been received describing similar cases in cattle.

Note.—A full description of this reaction was published in the Journal of the American Veterinary Association, Vol. 4, No. 1, April, 1917.

Fig. 28.—Non-fatal reaction following injection of Warble juice.

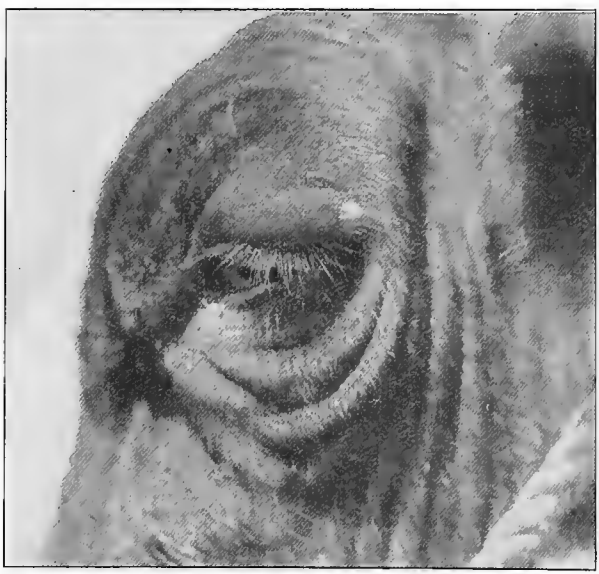

Fig. 29.—The same animal shown in Fig. 28. Enlargement of eye.

The Principal Differences Between the two Flies.

H. bovis.	*H. lineatum.*
1. Length 14 mm. Distance between eyes just in front of ocelli 1·9 mm., greatest diameter of eye 1·9 mm.	Length 12·7 mm. Distance between eyes just in front of ocelli 1·9 mm., greatest diameter of eye 1·6 mm.
2. Yellow hair on anterior part of thorax.	Anterior part of thorax black and shining.
3. Wing veins dark brown.	Wing veins nearly black.
4. Alulæ have a reddish brown border.	Alulæ are uniformly white.
5. Under part of abdomen and thorax nearly black.	Under part of abdomen and thorax lighter.
6. Legs clean with few hairs.	Legs rough and hairy.
7. Colouring of tail end, orange yellow.	Colouring of tail end, reddish orange.

Methods of Oviposition.

1. Lays in sunshine, principally from 10 a.m. to 4 p.m., but has been seen both earlier and later.	Lays principally in the shade of the animals, from about 10 a.m. to 4 p.m.
2. Causes cattle to "gad," both old and young.	Causes annoyance especially to young animals.
3. Lays its eggs principally when the animals are running.	Lays its eggs mostly when the animals are recumbent.
4. The eggs are laid mostly on the outside of the hind quarters and on the legs above the fetlocks.	The eggs are laid on all parts which the fly can reach when resting on the ground, *i.e.*, while the animals are lying down. Even when the animals are standing, the fly is able to lay eggs on those hairs which are close to the ground, namely, on the heels.
5. The fly is a clumsy insect and strikes at the animals blunderingly.	The fly is much more gentle and deliberate in its movements.
6. The eggs are laid singly at the roots of the hairs and are rarely visible without lifting the hairs.	Several eggs are attached to a single hair and are often visible without lifting the hair.

Skin Lesions.

Hypodermal rash. An irregular scattering of round raised lumps, especially on the outside of the hind quarters, appearing suddenly, anaphylactic in nature and rarely tending to suppurate. Very little exudation of serum.	Hypodermal rash. Diffuse irregular swellings, very irritable, appearing suddenly, anaphylactic in nature, often large and ending in the production of pus, and a marked dermatitis. The lesions follow the parts of the animal which come in contact with the ground, *i.e.*, legs, flanks and sternum. A large quantity of exudate mats the hairs.

Larva.

The segment in front of the spiracular segment unarmed.	The segment in front of the spiracular segment armed.

Summary.

Hypoderma lineatum lays its eggs as early as April 15, but the usual laying period is during the month of May. At Agassiz, they have never been captured later than May 30. *H. bovis* begins to lay in the early part of June and continues up to the beginning of August. Between the last appearance of *H. lineatum* and the first of *H. bovis* there is usually a period of ten days when the cattle are immune from attack of either species. *H. bovis* frightens the cattle much more than *H. lineatum*. The eggs take about a week to hatch; the larvæ bore through the skin in the coarser, porous parts, taking several hours in the process; at this stage they are about 1 mm. long. The lesions

resulting from this penetration are caused partly by anaphylactic reactions and partly by bacterial invasion, those produced by *H. lineatum* being the more severe.

For the skin lesions the name of *hypodermal rash* has been proposed.

At this point there is a hiatus in the life history. It is not positively known how the larvæ reach the œsophagus, where they are subsequently found; most likely they travel in the loose connective tissues under the skin up to the region of the throat and into the œsophagus where the muscles bifurcate. Passing down the œsophagus they follow the submucosa and are almost always found lying along the long axis of the canal. Whilst in the œsophagus, small œdematous swellings are found surrounding the grubs; these are sterile and are anaphylactic in character; the exudate contains large numbers of eosinophilic leucocytes.

The earliest record made at Agassiz of larvæ in the œsophagus was on August 15, when a larva 3·4 mm. was found and several slightly larger. Continental observers have recorded smaller larvæ than this.

H. lineatum makes its appearance in the backs of cattle about December 15, and *H. bovis* about a month later. The larvæ at this time have grown to about 1·5 cm., and are similar in size to those which are found in the neural canal and under the skin. At this stage it is difficult to separate the larvæ of the two species, but Bishopp has, recently, discovered good distinguishing marks between them. The life histories overlap at this period making it difficult to follow the migration, but in the latter part of the season (the middle of March) the last larvæ to leave the œsophagus are at the paunch end. They pass out under the pleura and go to the neural canal, either up the crura of the diaphragm, or up the posterior border of the ribs entering the canal by the posterior foramen. The larva evidently makes use of the canal as an easy means of access to the lumbar region, the part of the animal which is best suited for passing its last stages within the host.

The larvæ follow connective tissue exclusively and no larvæ have been discovered in muscular tissue.

The mature larvæ leave the animals' backs from the early part of the year up to the first days of July.

The periods for the two species have not been fully worked out; but, judging from what records there are of the pupal period and the time of year the flies are on the wing, *H. lineatum* begins to emerge in February and finishes about May 1. *H. bovis* begins about May 1 and ends approximately on July 1. The average pupal period for *H. bovis* is 32·5 days, and for *H. lineatum* a little less. The duration of the life of the flies is short, seeing that they cannot feed. This life history applies to Agassiz, British Columbia; doubtless in other countries variations will be noticed, but the period spent by the larvæ within the host must be of the same duration, seeing that animals' temperatures are the same the world over.

Prevention.—Animals should be housed during the heat of the day to prevent the flies laying upon them. Warble grubs should be squeezed out as early as possible during the year. This method will lessen the damage to animals and their hides. If the total eradication of the pest is attempted, co-operative measures must be undertaken.

ACKNOWLEDGMENTS.

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